Competition and predation between rainbow trout and largemouth bass in Crane Prairie Reservoir.

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Introduction

Faced with increasing angler pressure and recognizing opportunities presented by development of multiple use reservoirs, fishery managers developed the concept of a "two-story" fishery to increase utilization of available lentic habitat. With bass and other centrarchids inhabiting the shallow, warm littoral areas of a lake or reservoir and trout or walleye utilizing the cooler, deeper limnetic regions, managers could theoretically increase the production of gamefish from lentic habitats (Eddy and Underhill 1974).

Although there are many examples of the creation of successful "two-story" fisheries, biological and social issues often affect the outcome. The level of biological interactions, e.g., competition and predation, can determine the success of such a fishery, while the social acceptance of the program is often influenced by the preferences, biases and perceptions of the user groups. Crane Prairie Reservoir is a case in point. The historic capacity of this reservoir to produce large rainbow trout, *Oncorhynchus mykiss*, in excess of 10 pounds, from releases of hatchery-reared fingerling has been its claim to fame. Following the appearance of largemouth bass *Micropterus salmoides* in this blue-ribbon trout lake in the early 1980's, the production of trophy bass (in excess of 4 pounds) has been unmatched by any Eastern Oregon reservoir. However their presence has caused concern among management biologists and trout anglers. Predation of bass on stocked trout and possible decreases in trout growth and survival as a result of competitive interactions were identified as possible conflicts arising from an expanding bass population.

Social perception and unanswered biological questions led the Department to investigate this interaction in 1989 and 1990. That study provided information about some biological and social aspects of the fish community and fishery, but did not investigate the interactions throughout the entire growing season. The present study was designed to complement the previous study with several objectives:

1. Determine the extent to which various sizes oflargemouth bass consume stocked hatchery trout;
2. Investigate diet overlap between fingerling hatchery trout and largemouth bass; and
3. Assess whether competitive interactions with largemouth bass could be limiting the growth of stocked hatchery trout.

Study Site

Crane Prairie was a natural prairie located at the convergence of the upper Deschutes River, Cultus River, Quinn River, Rock Creek, Cultus Creek, and several other minor tributaries. The first Crane Prairie dam was constructed in 1922 by the Bureau of Reclamation. The present 36-foot high dam was constructed for irrigation storage in 1940. At full pool, the reservoir covers 4,167 acres, impounds 55,330 acre-feet of water, and has an average depth of 11 feet and a maximum depth of just over 20 feet (Johnson et al. 1985).

Timber was not cleared from the meadow and the adjacent lodgepole pine forest when the reservoir was impounded. These trees, now partially or totally submerged, provide excellent cover for fish as well as a tremendous amount of substrate for production of aquatic insects (King 1968). In addition, they provide perches for avian predators which may influence fish abundance and species composition in the reservoir (Lind 1976, Anderson 1985). Exposure and weathering of ordinarily submerged trees by low pool levels in recent years has accelerated the decay and loss of standing timber in the reservoir.

Tui chub *Gila bicolor* first appeared in the reservoir in 1953 and flourished in the shallow, productive water. By the early 1980s, they comprised over 80%, by number, of the reservoir fish community (personal communication, Ted Fies, Oregon Department of Fish and Wildlife, Bend District

Fish Biologist, Bend). Tui chub were the primary prey for largemouth bass, rainbow trout, and avian predators. Conditions associated with the recent drought - (reduced access to suitable spawning sites and increased predation due to decreased water volumes) - have caused the collapse of the chub population (personal communication, Ted Fies, Oregon Department of Fish and Wildlife, Bend District Fish Biologist, Bend). When they were abundant, tui chub were the predominant food item of largemouth bass greater than 200 mm (Shrader 1993). This has increased concerns of trout anglers regarding the quality of the trout fishery if bass switch their primary prey from the dwindling tui chub to stocked hatchery rainbow trout.

Methods and Materials

Fish were collected at approximately 2-week intervals between June and October, 1994 with an electrofishing boat. Bass > 200 mm collected early in the season were marked with a caudal punch. Subsequent recaptures allowed calculation of short-term, area-specific population estimates.

Hatchery rainbow trout released in Crane Prairie Reservoir were marked with an adipose fin clip and with oxytetracycline (OTC). The fish were fed TM-100, a veterinary grade of OTC, with their food for 2 weeks to achieve a cumulative dosage of 0.5 grams of OTC per kilogram of fish. OTC is deposited in the bone of actively growing fish and is discernible under ultraviolet light as a fluorescent band in vertebral sections (Weber and Ridgeway 1962, 1967). Thus hatchery trout that had been consumed by bass and were too badly decomposed to identify the adipose fin clip were identifiable using this technique.

Stomach contents of largemouth bass > 200 mm were recovered through gastric lavage followed by an inspection of the mouth and esophagus for large items not flushed clear. Stomach contents were rinsed through a sieve (1-mm opening) and preserved in 10% formalin. A sample of bass < 200 mm and rainbow trout were sacrificed and their digestive tracts were removed and preserved.

Food items were examined using a variable power (7-30X) binocular dissecting microscope and were identified to the lowest practical taxonomic level (most often to order, but in some cases, sub-order or family), and counted. In most cases separate tallies were kept for adult insects and their larval stages; dipterans, other than chironomid larvae, were the primary exception. Identification of partially digested fish remains to family was accomplished from diagnostic bones (Hansel et al. 1988)or vertebral columns (H. Hansel, U.S. Fish and Wildlife Service, unpublished data). Hatchery trout were distinguished from other salmonids by tetracycline marks in sections of vertebrae.

Percentage contribution to the diet (by volume) of each category of food item was calculated on the basis of the entire volume of food eaten by a category of gamefish (e.g., hatchery rainbow, 200-249 mm largemouth bass, etc.) sampled on a particular date. Volume of other specific food items consumed was calculated by multiplying the number of individuals by the average volume per individual. Average displacement (volume) per individual was measured by placing 10 to 20 representative individuals in a graduated centrifuge tube partially filled with water.

Estimates of Losses to Bass Predation

Loss of hatchery rainbow trout through largemouth bass predation was estimated by applying rates of consumption to the estimated population of each size class of bass (200-299 mm, 300-399 mm, and 400 mm and larger; APPENDIX A). Previous work (Shrader 1993) indicated that bass less than 200 mm did not prey on hatchery trout to an appreciable degree. Gastric evacuation rates (time to 90% digestion) were estimated from Markus (1932) and Cochran and Adelman (1982). The period of active predation on stocked trout was estimated from the presence of hatchery rainbow in bass stomachs collected during electrofishing samples. For purposes of estimation of bass predation on stocked trout, it was assumed that trout were preyed on for only the period when they were observed in bass stomachs. Calculation of digestion rates was based on average water temperatures of 16, 20, and 22°C for successive two week periods beginning on the date of first stocking.

Assessment of Competitive Interaction

Investigation of possible competitive interaction between stocked rainbow trout fingerlings and largemouth bass requires identification of significant diet overlap for prey items which are limited in abundance. This simplistic definition assumes no niche segregation has occurred between bass and trout to minimize competitive pressure.

Trout diet composition was described through collection of trout stomachs during routine electrofishing. Contents were analyzed in the same manner as previously discussed for bass stomachs. Diet overlap will be quantified using the Schoener index (Wallace 1981), which is calculated as follows:

$$\alpha = 1 - 0.5(\sum_{i=1}^{n} |p_{xi} - p_{yi}|),$$

where

n = number of food categories,

p_{xi} = proportion, by volume, of food category i in the diet of
    the length category of largemouth bass, and

p_{yi} = proportion, by volume, of food category i in the diet of
    stocked fingerling rainbow trout.

The resultant index ranges from a value of 0.0 to 1.0 and is considered to be biologically significant when the index exceeds 0.60 (Zaret and Rand 1971; Mathur 1977). The index for the rainbow trout/largemouth bass interaction will be calculated twice - with and without exclusion of rainbow trout in the bass diet.

Prey availability or abundance was assessed indirectly using bioenergetic simulations of the patterns of trout growth. The index output by the model, a P-value, is a proportionate measure of how a species' observed consumption approaches its theoretical consumption (as limited by the ambient thermal regime). In the absence of physical limiting factors, if the P-value of a species is substantially below 1.0, then there is the possibility that growth is being limited by competition. Parameters for the chinook salmon bioenergetic model of Hewett and Johnson (1987) were modified for rainbow trout (Rand et al. 1993). Values for caloric densities of prey species were obtained from Richman (1958), Davis and Warren (1971), and Hewitt and Johnson (1992).

Water temperatures used for bioenergetic modeling were a combination of recorded and estimated values. Estimated temperatures were checked against onsite water temperatures recorded during sampling.

Results

Rainbow Trout and Largemouth Bass Diet Composition

Stocked rainbow trout consumed a variety of prey items (Table 1), reflecting their categorization as generalists or opportunistic feeders (Calhoun 1966, Scott and Crossman 1973). Amphipods, damselflies, snails, zooplankton, caddisflies, or chironomids were important prey items of stocked rainbow trout at one time or another during the year (Table 1). The importance of different taxa of prey to largemouth bass varied with the size of the fish and the month (Table 2). Diet summaries of bass > 400 mm are based on inadequate samples and are not presented. Largemouth bass less than 200 mm did not consume hatchery rainbow trout (Table 2). Invertebrates, primarily amphipods, mayflies, dragonflies, damselflies, and chironomids, were the major prey of these small bass, although stickleback were occasionally an important prey item of bass greater than or equal 200 mm (Table 2).

Hatchery rainbow trout were an important component of the diet of bass > 200 mm in June and July, composing up to 67% of the diet of 300-399 mm bass in June (Table 2). Higher water temperatures in the littoral areas during August forced rainbow trout to abandon that habitat, as evidenced by their absence in electrofishing samples. In August and September, amphipods and three-spined stickleback became the prevalent prey of 200-299 mm bass. Large prey items, crayfish and salmonids other than hatchery rainbow trout (hatchery kokanee, hatchery and wild brook trout, and wild rainbow trout and whitefish) comprised the bulk of the diet of 300-399 mm bass from July through September. The percentage of empty stomachs increased significantly in October sampling, suggesting that bass were not feeding actively as water temperatures dropped below 10°C.

Loss of Hatchery Rainbow Trout to Bass Predation

Based on the 1994 length frequency distribution (Figure 1), the estimated 11,000 largemouth bass would be distributed as follows: 9,706 bass between 200 and 299 mm, 1,114 bass between 300 and 399 mm, and 179 bass greater than or equal to 400 mm.
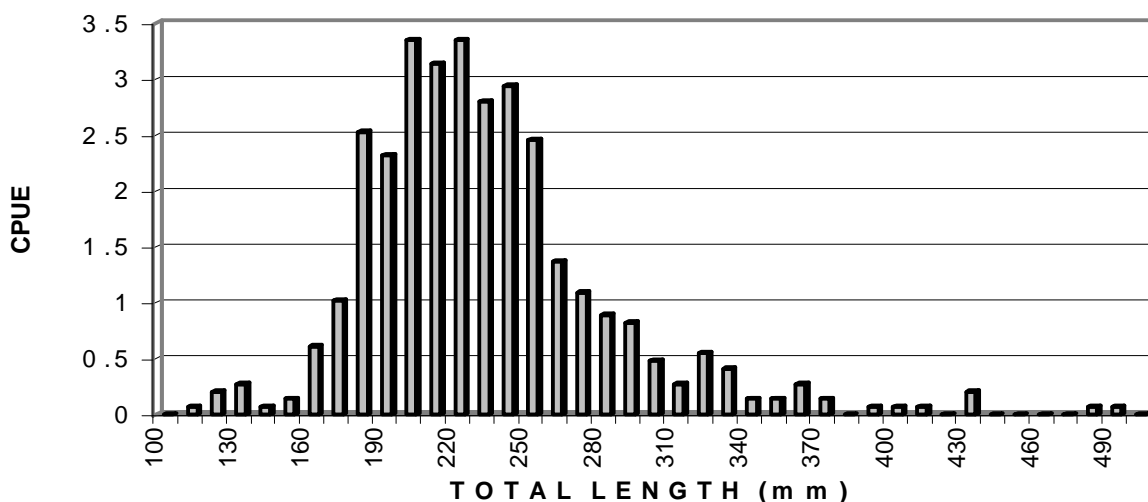

Figure 1. Length frequency distribution of largemouth bass captured by electrofishing from Crane Prairie Reservoir in 1994. Catch-per-unit-effort (CPUE) expressed as number of bass captured for every 1000 seconds of electrofisher time.

The rate of bass predation on stocked trout was not consistent across the reservoir. Bass in the area of Crane Prairie Resort preyed more heavily on hatchery trout immediately following stocking (1.0 trout per 200-299 mm bass and 2.0 trout per 300-399 mm bass) than did bass in the rest of the reservoir (0.026 trout per 200-299 mm bass and 0.045 trout per 300-399 mm bass). Predation on hatchery trout immediately following stocking at other stocking sites (Rock Creek and Quinn River ramps) was not different from rates seen after trout had dispersed. As a result, predation loss was calculated separately for the "Resort" subpopulation immediately following stocking and the entire Crane Prairie bass population for the remainder of the year.

The "Resort" subpopulation of bass was estimated at 2,134 fish based on mark-recapture results (Appendix A). Allowing four days for hatchery trout to disperse following stocking at the Resort ramp (personal communication, Ted Fies, Oregon Department of Fish and Wildlife, Bend District Fish Biologist, Bend; Wurtsbaugh and Tabor 1989), an estimated 4,784 trout were eaten by "Resort" bass

(APPENDIX A). Stocking at the resort ramp was terminated after this high loss at that site was initially exposed.

The rate of bass predation on hatchery trout varied with the peak rate seen in June (which coincided with stocking of hatchery trout on June 7, 14, 23, and 24). Hatchery trout were found in bass stomachs on July 7 and not on the next sample occasion (August 4). The estimated number of hatchery trout consumed by bass (including those from the single plant at the Resort ramp) was 13,954 fish, or 6.8% of the hatchery fish stocked (Appendix A).

Bass consumption of salmonids other than hatchery rainbow was examined using the same methodology discussed above. The inability to identify partially-digested stomach contents beyond family did not allow segregation and calculation of species-specific predation losses. An estimated 15,284 wild rainbow and mountain whitefish, wild and hatchery brook trout, and hatchery kokanee Oncorhynchus nerka, were eaten by largemouth bass from May through October.

Bioenergetic Modeling of Trout Growth

The P-values obtained for rainbow trout stocked on June 7 ranged from 0.53 to 0.84 (Table 3). These values should be considered as minimum P-values as trout stocked after June 7 were probably included in the endweight calculations. In addition, anglers began to harvest some of the larger hatchery trout by the end of September. This harvest could have reduced the observed P-value for the period August 4 to October 4 by reducing the average size of fish available for our sample.

Estimation of Diet Overlap

Schoener overlap indices varied monthly and with the size category of bass (Table 4). Diet overlap between stocked rainbow trout and largemouth bass never exceeded 0.60 for those months when adequate fish were collected.

Discussion

The idealized concept for a two-story fishery assumes a lake's production is optimized by partitioning of habitat between trout and bass. In reality the littoral and pelagic zones are not compartmentalized - water, nutrients, and fish can and do move dynamically throughout the entire lake (Johannes and Larkin 1961). Competition and predation are direct interactions that may occur between trout and bass during periods of spatial overlap. Conditions in 1994 - low water levels and the disappearance of the tui chub - were almost optimal for estimating the maximum effect of bass on hatchery trout.

Table 1. Diet composition, by percentage of total volume consumed, for rainbow trout in Crane Prairie Reservoir, 1994. Sample size (n) reflects actual number of stomachs examined that contained food.

Month	n	Amphipods	Damselfly	Dragonfly	Snails	Zooplankton	Mayfly	Caddisfly	Other
June	7	11.3	37.4	0.0	0.0	13.3	0.0	16.1	21.9[a]
July	11	44.2	4.8	0.0	0.0	5.8	6.0	2.2	37.0[b]
August	13	24.9	0.4	0.0	54.4	0.0	0.6	3.2	16.5[c]
September	14	19.5	0.3	0.0	4.1	29.4	0.5	31.6	14.6[d]
October	9	12.7	8.1	4.4	55.5	17.1	0.0	0.0	2.2

[a] Miscellaneous insects (7.7%), stoneflies (9.9%), and water striders (4.3%).
[b] Miscellaneous insects (33.6%), stoneflies (1.9%), and water striders (1.5%).
[c] Miscellaneous insects (16.0%), and leeches (0.5%).
[d] Miscellaneous insects (14.6%).

Table 2. Diet composition, by percentage of total volume consumed, for largemouth bass in Crane Prairie Reservoir, 1994. Sample size (n) reflects actual number of stomachs examined that contained food.

Month	n	Hatchery Rainbow	Other Salmonids	Stickle back	Zooplankton	Amphipod	Caddis fly	May fly	Damsel fly	Dragon fly	Cray Fish	Other
0-99 mm largemouth bass[a]												
July	5	0.0	0.0	0.0	0.0	7.3	3.1	72.1	17.3	0.0	0.0	0.2
August	4	0.0	0.0	0.0	0.0	38.2	0.0	0.0	60.6	0.0	0.0	1.2
100-199 mm largemouth bass												
June	1	0.0	0.0	57.4	0.0	0.0	0.0	42.6	0.0	0.0	0.0	0.0
July	4	0.0	0.0	0.0	0.0	42.4	0.0	5.1	10.0	29.6	0.0	12.9[b]
August	16	0.0	0.0	6.0	0.0	28.0	0.0	15.8	9.4	0.0	0.0	40.8[c]
September	20	0.0	0.0	60.0	0.0	9.4	0.0	0.4	23.2	0.0	0.0	7.0
October	2	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
200-299 mm largemouth bass												
June	27	41.0	4.0	14.7	0.0	1.5	0.0	0.2	21.2	3.6	11.0	2.8
July	10	36.0	0.0	0.7	0.0	2.3	0.0	8.1	6.2	30.7	0.0	16.0[d]
August	44	0.0	0.0	25.9	0.0	45.3	0.0	1.3	0.6	7.4	7.4	12.1[e]
September	26	0.0	2.5	70.7	0.0	2.0	0.0	0.0	1.5	8.9	0.0	14.4[f]
October	17	0.0	0.0	11.0	0.0	20.2	0.0	0.7	3.2	7.1	5.4	2.4
300-399 mm largemouth bass												
May	26	0.0	4.8	16.3	0.0	9.0	0.0	1.3	33.8	26.7	0.0	8.1
June	13	67.8	10.1	2.1	0.0	0.3	0.0	0.0	15.5	2.4	0.9	0.9
July	7	10.7	87.5	0.0	0.0	0.1	0.0	0.4	0.4	0.0	0.0	0.9
August	16	0.0	0.0	5.3	0.0	0.8	0.0	0.0	0.2	0.0	92.1	1.6
October[g]	4	0.0	73.8	2.0	0.0	0.8	0.0	0.0	0.0	4.1	0.0	19.3[h]

[a] No 1-99 mm largemouth bass were collected in June, September, and October.
[b] Miscellaneous insects (10.3%), and snails (2.6%).
[c] Miscellaneous insects (21.8%), snails (11.8%), and unidentified fish (7.2%).
[d] Leeches (11.2%), and miscellaneous insects (5.0%).
[e] Snails (5.2%), miscellaneous insects (4.3%), and leeches (2.3%).
[f] Snails (6.2%), miscellaneous insects (5.9%), and unidentified fish (2.2%).
[g] Includes 1 fish collected in September.
[h] Unidentified fish (19.1%), and miscellaneous insects (0.2%).

Table 3. P-values generated from bioenergetic modeling of growth of hatchery rainbow trout from June 7 to October 4, 1994 in Crane Prairie Reservoir.

	Deschutes Channel	Littoral Area
June 7 – August 4	0.53	0.53
August 5 – October 4	0.79	0.84

Table 4. Monthly Schoener diet overlap indices for rainbow trout and different size categories of largemouth bass from Crane Prairie Reservoir, 1994. Monthly index was not calculated if 2 or fewer fish were collected.

Size of bass (mm)	June	July	August	September	October
1-99	--	0.29	0.38	--	--
100-199	--	0.40	0.55	0.34	--
200-299	0.47	0.17	0.43	0.16	0.30
300-399	0.43	0.35	0.27	--	0.05

Stress related to handling during transport and stocking has been shown to create behavioral changes in trout which can decrease their ability to reach cover (Sigismondi and Weber 1988) and increase their vulnerability to predation (Ayles et al. 1976; Barton et al. 1980, 1986). Over a third of the trout fingerlings lost to predation were consumed by largemouth bass immediately following stocking at the resort ramp. However, our sampling was not able to detect any difference between the level of predation occuring in the vicinity of the Rock Creek and Quinn River stocking sites immediately before and after stocking of trout. In contrast to the area around the Resort ramp, these areas possessed high structural complexity - abundant woody debris and large rocky substrate - which probably provided trout refugia from predation (Glass 1971; Crowder and Cooper 1982; Savino and Stein 1982).

Hatchery trout were not a dominant food item in the diet of largemouth bass following the initially high levels seen following stocking. This is in spite of trout and largemouth bass being often found in the same habitat during our sampling. Night electroshocking probably secured a good representation of bass consumption of trout as bass feeding peaks during crepuscular periods (Reynolds and Casterlin 1976; Helfman 1981) and calculated gastric evacuation times were greater than 24 hours. Even though hatchery trout are extremely naive with respect to predation and bass are successful in 90% of their attacks (Nyberg 1971), trout quickly learn to incorporate predation risk into their behavioral strategies (Tabor and Wurtsbaugh 1989). Tabor and Wurtsbauch (1989) demonstrated that the addition of predators (brown trout) to a pond caused juvenile rainbow trout to stop actively foraging and seek cover in inshore areas. Once they adjusted to their new environment, trout undoubtedly used the abundant cover in Crane Prairie (woody debris, vegetation, and rocky substrate) to reduce their exposure to bass predation.

Definitive proof of competition for food between largemouth bass and hatchery trout must show a shared utilization of a limited resource. P-values generated through modeling of rainbow trout growth suggest some factor(s) is limiting trout from reaching their potential during the period from June 7 to August 4. Diet overlap indices suggest that the levels of overlap occuring are not biologically significant. So given these results, are largemouth bass and rainbow trout competing for food?

Identification of the nature and extent of competition between bass and trout is an important, albeit, difficult interaction to quantify. Niche segregation by species can confound in situ investigations of competition for food based on diet overlap (Abrahams 1996) - our study did not estimate fingerling trout preferences or diet in the absence of bass. What we saw was the diet as a result of any interaction or segregation developed to reduce competitive pressure. Ideally the diet of both species would have been investigated with and without the other species present and then compared. Stocked rainbow trout consumed a variety of prey items, reflecting their categorization as generalists or opportunistic feeders (Calhoun 1966, Scott and Crossman 1973). This plasticity probably reduces the negative effects of any

competitive interaction with bass, but the question remains to what extent are fingerling trout consuming what they prefer or what they are being "forced" to eat as a result of interaction with bass. Our use of bioenergetics and diet overlap is a powerful method in confirming the lack of competition, i.e., P-value close to 1, but is substantially less effective in confirming its presence. If the P-value is less than 1, then competition is just one possible explanation. Given the limitations of our study, there is no way to evaluate this.

Another possibility for the lower initial P-value of stocked trout could be due to a reduction in feeding efficiency due to a novel environment. Condition of hatchery rainbow decreased substantially through July before increasing in August. This could have reflected a period of adaptation to to foraging in a natural environment.

One provocative explanation for the results of the bioenergetic modeling was that trout behavior to reduce the risk of predation affected their ability to consume food. The difference in the rate of predation losses between the resort site (little or no cover) and the other two sites (abundant cover) suggests that rainbow trout are taking advantage of the cover in the reservoir to reduce the predation risk. Juvenile salmonids are considered energy maximizers (Dill et al. 1981; Bachman 1984), which means they only have a fixed amount of time to feed and to obtain as much energy as possible (Pyke et al. 1977). Predator avoidance behavior by juvenile trout could reduce the time available for feeding and result in the inability to consume as much as their metabolic rate will allow. Wilzbach (1985) demonstrated that in the presence of predators, stream-dwelling adult cutthroat trout *Oncorhynchus clarki* were more apt to stay associated with cover when food abundance was high than low. This scenario could explain the reduced P-value despite the lack of biologically significant levels of diet overlap.

Growth of hatchery rainbow trout in Crane Prairie Reservoir, therefore, may be limited not by food or competition, but by a shift in the foraging strategies of trout in response to predation risk from largemouth bass and/or birds. Prey species will frequently alter their foraging behavior or strategy, often at a energetic loss, to balance a perceived predation risk (Dill 1983; Dill and Fraser 1984; Gotceitas and Colgen 1987). Predator avoidance by *Campostoma anomalum*, an algal-grazing minnow, constrained their feeding efficiency and allowed algal abundances to increase in stream pools (Powers et al. 1985). Werner et al. (1983) found that bluegill *Lepomis macrochirus* limited their habitat use to areas of low foraging profitability when a predator, largemouth bass, was present and, as a result, grew more slowly than when no predators were present.

The increase in the P-value during the latter period examined (August 4 - October 4) coincides with the elimination of predation risk for most of the trout. By mid-August, the influence of predation on the distribution of stocked trout was diminished or eliminated as most of the hatchery trout had grown too large to be consumed by the bass present in the reservoir. Thermal segregation of the two species may have also contributed to the increased P-value, but this separation was only apparent for a short amount of time. Decreased predation risk allowed greater optimization of foraging, negating the benefits associated with cover. Mittlebach (1981) shows that small bluegill chose to stay in the less rewarding vegetation to reduce predation risk, while larger bluegill, too big to be preyed upon, foraged in the pelagic area with impunity. Decreased predation risk could have allowed Crane Prairie trout to consume closer to the metabolic capability during the latter part of the summer.

Bioenergetic modeling offered a bridge for addressing the question of competition through collection of basic biological and physical information. However, there are some problems associated with this kind of modeling. When using the model, it is easier to determine when competition is not occuring, i.e., the P-value is close to one. As we have seen, when the resultant P-value is less than one, competitive limitation is only one possible explanation. Also, parameters used in modeling are subject to errors and biases which can affect the results. Lewis and Helms (1964) demonstrated that vulnerability to bass predation within a species varied due to size of bass and prey. Size-selective predation of smaller rainbow trout could positively bias estimates of growth in this study. Gear selectively for larger fish could have also positively bias estimated growth. Conversely, inclusion in samples of rainbow trout stocked after June 9 could negatively bias growth estimates and resultant P-values. Angler harvest of faster-growing (larger) fish in September and October could have also negatively biased growth estimates and resultant P-values by shifting the average size of trout left in the reservoir downward. Higher water temperatures during the latter period examined could have increased the activity of trout and/or prey items, thus making them more vulnerable and accessible to predation. Errors in temperature could have affected results but P-values were fairly robust in trials where possible differences were

modeled. Despite all these problems, bioenergetic modeling was the most feasible methodology to make a qualitative assessment of competition given the constraints this study was conducted under.

The dynamics of the hatchery trout program have undoubtedly changed in response to the reduction in tui chub. Abundant tui chub populations in other waters, Diamond Lake for instance, have negatively affected trout programs and often resulted in chemical rehabilitation of the lakes. Bass predation was probably a factor in the demise of the chub population, but it is unlikely that it was solely responsible given the relative dispersal rates of both species (Crowley 1981). Reduced access to good spawning habitat due to drought-related low water levels undoubtedly contributed to the disappearance of tui chub in the reservoir.

Management Implications

Interactions between largemouth bass and rainbow trout in Crane Prairie Reservoir do not negate co-management of both species under present conditions. Information gained from this study, primarily predation rates, can be used to estimate the direct effects of changes in largemouth bass population structure on predation losses of rainbow trout. The 1989-90 study suggested that there is about a 8.5% return to the creel on hatchery rainbow trout stocked in Crane Prairie. The 9,172 trout consumed by "non-Resort" bass in 1994 translates to about 778 trout lost to the angler creel or a 6% reduction in trout harvest. This is in exchange for the recreation associated with catching over 29,000 largemouth bass. Future trout losses due to predation can be estimated using bass predation rates generated from this study. Higher water levels and/or increases in the tui chub or largemouth bass population sizes would undoubtedly affect the accuracy of these estimates, but they could be used as estimates of maximum rates of consumption.

The theory that a perceived largemouth bass predation risk has reduced the foraging efficiency of rainbow trout is one of several explanations of the study results. If this hypothesis is valid, it should result in reduced growth and survival, but District sampling has not noted any appreciable change in the success of the hatchery program. It is questionable, however, given the sensitivity of the sampling program, whether it could detect a small change attributable to competitive interaction with bass. It is possible that the altered foraging behavior occurs for such a short time (two months) that it results in no measurable change in trout survival and, ultimately, the fishery.

Competition is an important interaction to consider when discussing bass management at Crane Prairie. The productivity and diversity of prey in Crane Prairie Reservoir may reduce competition for food between hatchery trout and largemouth bass, but results of our study were inconclusive. The variable we were unable to investigate was the effects of an abundant tui chub population on this system. The fish community in Crane Prairie is dynamic and effects at one level can cause cascading changes throughout the system. Given the importance of tui chub in the diet of Crane Prairie largemouth bass (Shrader 1993), a decrease in chub numbers has probably lead to increased consumption of trout by bass. This loss to the trout fishery may be offset by decreased competition with a reduced tui chub population (due, in part, to bass predation), but complicated by the reduced availability of chub for large trout. In addition to the possibility of direct competitive interactions with chub, trout may alter their behavior in the presence of an abundant tui chub and accept more of a predation risk while feeding. Dill and Fraser (1984) have shown that in the presence of competitors, juvenile coho salmon decreased their response to predation risks while feeding. This suggests that if bass had not reduced chub numbers, trout might have been more active and, therefore, more vulnerable to bass predation. How this myriad of indirect interactions balance out is beyond our ability to predict. As a result, we must restrict our estimation of management effects to a very gross level.

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APPENDIX A

Estimation of Stocked Hatchery Rainbow Trout Lost Through Predation by Largemouth Bass at Crane Prairie Reservoir

Hatchery trout consumed by "Resort" bass:

      Estimated population = 2,134 bass, which equates to
                            1,876   200-299 mm bass,
                             232   300-399 mm bass, and
                             25   bass > 400 mm.
      Consumption rates =
                    1 stocked trout / 200-299mm bass, and
                    2 stocked trout / bass > 300.

      Digestion rate of 1 trout for a 250 mm bass =
                    approximately 24 hours @ 18°C.

      NOTE: Although comparable information for largemouth bass is not available, a 250 mm smallmouth bass digests 1 trout at the same rate that a 350 mm smallmouth digests 2 similar sized trout.

      Assuming that it takes stocked trout 4 days to disperse from the stocking site and that predation loss decreases linearly from a maximum on the day of stocking to zero 4 days later, then trout mortality due to predation is:

                Day 1   2,392 trout;
                Day 2   1,594 trout;
                Day 3   796 trout; and
                Day 4   0 trout
                TOTAL 4,782 trout consumed by "Resort" bass.

Hatchery trout consumed by remainder of reservoir bass:

      Estimated 1994 Crane Prairie Reservoir largemouth bass population = 11,000 fish > 200 mm.

      This is based on a proportional relationship between the 1989 electrofishing CPUE (25.46) and average population estimate (10,530) and the 1994 electrofishing CPUE (26.6).

      Based on an estimated 11,000 bass greater than or equal to 200 mm and the 1994 electrofishing CPUEs, the 1994 population (minus the "Resort" subpopulation) consists of:
                    7,830 200-299 mm bass,
                     882 300-399 mm bass, and
                     154 bass > 400 mm.

Consumption rates =
          0.026 stocked trout per 200-299 mm bass = 206 trout/meal,
          0.045 stocked trout per 300-399 mm bass = 40 trout/meal; and
          0.333 stocked trout per bass > 400 mm   = 77 trout/meal.

Average digestion time @ 16°C = 49.5 hours;
                        @ 20°C = 34.0 hours; and
                        @ 22°C = 28.5 hours.

Size of   Number Trout   Trout consumed over a 14 day period
 Bass   of   per

(mm)	bass	meal	16°C	20°C	22°C
200-299	7,830	206	1,398	2,030	2,423
300-399	882	40	271	394	470
>400	154	77	522	759	905
			2,191	3,183	3,798

Therefore, total loss of hatchery trout to non-Resort bass = 9,172 fish.

Estimate of total loss of hatchery rainbow trout to largemouth predation:

Total loss of hatchery trout to non-Resort bass = 9,172
Total loss of hatchery trout to Resort bass   = 4,782
Total loss of hatchery trout to bass predation = 13,954 or 6.8% of stocked rainbow trout

Using the same methodology an estimated 15,284 wild salmonids were consumed by bass.